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Seasonal and Spatial Patterns of Ichthyoplankton Abundance in Elkhorn Slough, California

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Seasonal and spatial patterns in abundance of fish eggs and larvae are described from 323 samples collected from September 1974–September 1976 in Elkhorn Slough, a shallow, tidal embayment in Monterey Bay, California. These included 3645 larvae of 29 taxa that were numerically co-dominated by gobiid and clupeoid larvae. Ninety-four percent of the total catch comprised seven species, and included, in rank order abundance, *Gillichthys mirabilis*, *Engraulis mordax*, *Clevelandia ios*, *Hypomesus pretiosus*-osmerid, *Leptocottus armatus*, *Genyonemus lineatus*, and *Clupea pallasii*. Eggs of *E. mordax*, *Citharichthys* spp., and *G. lineatus* accounted for 73% of the catch.

Two seasonal groups of larvae were evident. *E. mordax* and the gobiids (*G. mirabilis* and *C. ios*) formed a summer–fall group. While more speciose, a winter and early-spring group comprised of larval *L. armatus*, *H. pretiosus*-osmerid, Atherinidae and *Ammodytes hexapterus* was not as abundant as the summer–fall assemblage. Egg densities were overwhelmingly high in summer, due almost entirely to *E. mordax*.

Similarity in species composition was greatest between collections from the most inland stations; larval assemblages from near-ocean stations were least similar to the inland slough assemblages. These distributions are attributed to reproductive specializations (egg type and spawning origin of adults) and hydrographic conditions.

Introduction

Early life of many nearshore marine fishes is spent in estuaries and shallow embayments (Pearcy & Myers, 1974; Weinstein, 1979; Powles *et al.*, 1984; Gunderson *et al.*, 1990). Year-class success of marine fish populations depends on survival during early developmental stages. Houde (1987) suggested relatively small variations in growth and mortality during early life may produce large fluctuations in fish recruitment. High prey availability,

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water temperature, and turbidity, and decreased water depth and turbulence in coastal embayments can enhance growth, limit predation, and increase the survival of young fishes (Blaber & Blaber, 1980; Blaber, 1985; McGowan, 1986). Many species are transient members of estuarine ichthyofauna, and transport primary production from these land-based ecosystems to coastal marine habitats after their first year of life (Weinstein & Walters, 1981; Allen, 1982). The contribution of these highly productive areas to coastal marine fish populations remains largely unknown.

Bays and estuaries of California are few in number and relatively small; their total area is less than 15% that of Chesapeake Bay (Horn & Allen, 1976). Greater than 75% of California's coastal wetlands have been lost through diking, filling, pollution and other degradations (Onuf *et al.*, 1978). Elkhorn Slough, a member of the National Estuarine Research Reserve System, is the largest wetland habitat south of San Francisco Bay on the central California coast. From studies of juvenile and adult fishes (Barry & Cailliet, 1981; Yoklavich *et al.*, 1991), the slough has been identified as spawning and nursery grounds for several species of marine fishes, as well as permanent home to at least six resident species. Although many of its resources are protected, continued erosion from breakage of dikes, wetland restoration activities, and strong tidal scour (Wong, 1989), and potential hydrographic and climatic changes (e.g. Onuf & Quammen, 1983) could impact this nursery area.

The principal objective of this study was to assess patterns of seasonal and spatial abundance of fish eggs and larvae in Elkhorn Slough. Additionally, we evaluate the influence of reproductive modes of adult fishes and physical characteristics of the environment on patterns of larval species composition. This study provides information prerequisite to long-term monitoring of ichthyoplankton assemblages in central California embayments, and for generating testable hypotheses regarding potential changes in these assemblages.

Study area

Elkhorn Slough (36°48'N, 121°47'W) is a shallow, tidal embayment and seasonal estuary at the head of the Monterey submarine canyon. It has an axial length of about 10 km, and a relatively small drainage basin of 585 km^2 (Figure 1; Browning, 1972). During our study, water depth of the main channel below mean lower low water (MLLW) ranged from about 5 m at the slough entrance to less than 2 m at the most inland station (Smith, 1973; Broenkow, 1977). Semidiurnal tides with a mean tidal range of 1·1 m result in well-mixed water in two environmentally distinct zones of the slough (Broenkow, 1977). The area above the mean tidal prism, which is about 4·8 km inland, has a water residence time in excess of 300 days. Salinity in this area varies seasonally with evaporation, precipitation and runoff, and ranges from 17‰ in March to 37‰ in June. Water temperature ranges from 12 to 26 °C. Water west of the tidal prism, representing about 75% of the mean high water volume, is exchanged daily and reflects nearshore ocean conditions, with cooler temperatures (12–18 °C) and more constant salinity (29–34).

Materials and Methods

Ichthyoplankton were collected monthly from September 1974–September 1976 at five stations located at the entrance to Moss Landing harbour, and approximately 0·6 (the bridge station), 3·1 (the dairy station), 5·4 (the red house station and present site of the

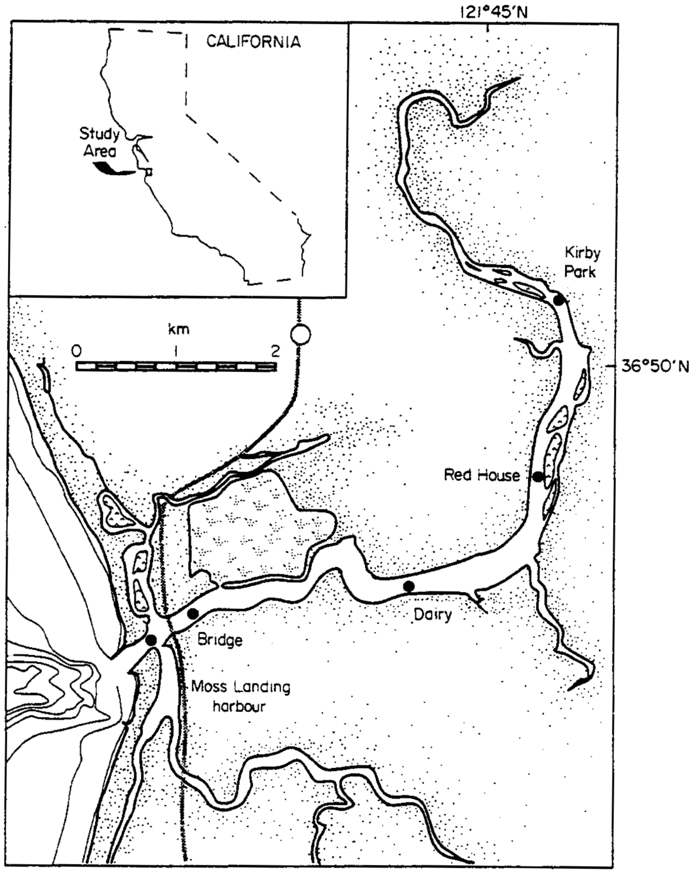

Figure 1. Larval fish sampling locations in Elkhorn Slough, CA.

Elkhorn Slough National Estuarine Research Reserve), and 7·9 km (the Kirby Park station) inland (Figure 1).

Larval fishes were collected with a 0·5 m diameter, 2·2 m long, zooplankton net (405 μm mesh). The net was attached to a frame and pushed in front of a 5 m Boston Whaler, thereby reducing net avoidance and disturbance in shallow water. Mean filtering efficiency of the net was estimated with flow meters to be 89·1%, and was comparable to a suggested minimum value of 85% (Tranter & Smith, 1968). The net was fished mid-channel in a straight line between permanent station marks (137–297 m apart) at a constant speed (2 knots) and depth (about 1 m below the water's surface). Duration of each tow was recorded. Sampling was conducted during daytime in a specific sequence from the bridge to the Kirby Park station, and only at high slack tide to reduce the effect of tidal surge. The harbour entrance station was sampled on adjacent dates because we could not sample all five stations during a single high tide.

Initially, two replicate samples were collected at each station. After May 1975, four samples were taken each month because plots of cumulative number of species against a randomly pooled number of samples indicated more replicates were needed to adequately sample all species. Dominant species, however, were not affected. Data were pooled by seasons, defined as fall (August, September, October), winter (November, December, January), spring (February, March, April), and summer (May, June, July). These groupings approximated the climatic seasonality of the study area in terms of rainfall, air and water temperature, and salinity (Broenkow, 1977).

Samples were preserved in the field with 10% formalin in seawater. Larval fishes were removed from all samples and stored in 5% buffered formalin. Fish eggs were sorted only from samples collected during the second year (October 1975–September 1976). Fish eggs and larvae were identified to the lowest taxa. Numbers of larvae of each species were standardized to 1000 m^3 of water filtered. Density of eggs was expressed as number per m^3. Larvae of good condition were measured to the nearest 0·5 mm (standard length).

We categorized larval species by egg types (demersal, pelagic and live-bearing) and spawning origin of the adult: resident (R: spawns and completes entire life in the slough); partial resident (PR: primarily lives in the slough, seasonally or ontogenetically moves to the ocean, and returns to reproduce in the slough); marine immigrant (MI: primarily lives in the ocean, and regularly spends some life stage in the slough); or marine (M: coastal species that rarely or never penetrates the inland slough area). Members of the R and PR categories potentially can spawn and complete their life cycle outside the slough environment. Studies on life histories of fishes in west coast estuaries (NOAA, 1990), and guides to early life stages of northeast Pacific fishes (Wang, 1981; Matarese *et al.*, 1989) were used to classify some species.

Species composition was compared between stations using the percentage similarity index (PSI; Krebs, 1989):

$$\mathrm{PSI} = \sum \mathrm{minimum}\,(p_{1i}, p_{2i})$$

where PSI is the sum of the smallest percentage by number (p_{1i} and p_{2i}) of each pair of species i from stations 1 and 2 respectively. This index ranges from 0·00 (no similarity) to 1·00 (identical species arrays). In the present study, PSI values greater than 0·60 were interpreted as significant, based on level of significance of product-moment correlation coefficient relative to PSIs (Cailliet & Barry, 1978). Additionally, Spearman's rank correlation coefficient, r_S (Sokal & Rohlf, 1981) was used to statistically compare rank order of species abundance between pairs of stations.

Results

Distribution and abundance of larvae

A total of 3645 larval fishes, representing 29 taxa from at least 17 families, was collected in 323 tows at five stations in Elkhorn Slough and adjacent harbour area. The only identifiable osmerids were post-flexion larval and juvenile *Hypomesus pretiosus* (surf smelt). We assumed younger larval osmerids were of this species also, but classified all as *H. pretiosus*-osmerid complex. Atherinid fishes probably included larvae of both species that spawn in the slough, *Atherinops affinis* (topsmelt) and *Atherinopsis californiensis* (jack smelt).

Seven species accounted for 94·0% of all larvae taken throughout the study (Table 1). The family Gobiidae comprised over 50% of the total catch; *G. mirabilis* (longjaw mudsucker) were the most abundant larvae.

Species composition and abundance varied seasonally and spatially. The greatest number of species occurred at the harbour entrance station, where 501 larvae of 20 taxa were

TABLE 1. Rank order abundance and size of fish larvae collected in Elkhorn Slough from September 1974 to September 1976. Adult life style was categorized as resident (R), partial resident (PR), marine immigrant (MI), and marine (M). Egg type of the adult was classified demersal (D), pelagic (P), or live-bearing (LB)

Taxa	Total catch N	Total catch %	Modal Length (mm)	Modal Frequency (%)	Length range (mm)	Adult life style	Egg type
Gillichthys mirabilis	1476	40·5	3	95·7	2–8	R	D
Engraulis mordax	864	23·7	3	15·7	2–33	MI	P
Clevelandia ios	353	9·7	3	59·7	2–15	R	D
Hypomesus pretiosus-osmerid	220	6·0	4	35·9	3–50	MI	D
Leptocottus armatus	206	5·7	5	31·0	3–11	R	D
Genyonemus lineatus	162	4·4	2	73·5	2–4	M	P
Clupea pallasii	144	4·0	6	14·7	3–28	MI	D
Neoclinus uninotatus	42	1·2	4	97·2	4–5	M	D
Citharichthys spp.	33	0·9	2	100·0	2	MI	P
Atherinidae	31	0·9	8	48·2	5–10	PR	D
Ammodytes hexapterus	20	0·5	4	85·7	4–5	M	D
Clinidae type I	11	0·3	3	57·1	3–4	?	D
Gobiidae type I	8	0·2	3	50·0	2–4	R	D
Sebastes spp.	8	0·2	3	62·5	3–21	M	LB
Stenobrachius leucopsarus	3	0·1	4	60·0	4–5	M	P
Psettichthys melanostictus	2	0·1	3	100·0	3	M	P
Coryphopterus nicholsi	1	—	2	100·0	2	M	D
Gobiidae type II	1	—	4	100·0	4	R	D
Clinocottus sp.	1	—	4	100·0	4	M	D
Gibbonsia sp.	1	—	10	100·0	10	M	D
Cebidichthys violaceus	1	—	9	100·0	9	M	D
Sebastes paucispinis	1	—	3	100·0	3	M	LB
Platichthys stellatus	1	—	6	100·0	6	MI	P
Lyopsetta exilis	1	—	3	100·0	3	M	P
Pleuronichthys verticalis	1	—	3	100·0	3	M	P
Bathylagus ochotensis	1	—	8	100·0	8	M	P
Oxyjulis californica	1	—	3	100·0	3	M	P
Paralichthys californicus	1	—	5	100·0	5	MI	P
Syngnathus leptorhynchus	1	—				R	LB
Unidentified fish larvae	49	1·3					
Total	3645						

collected in 44 samples. Mean monthly densities of larvae at the harbour entrance station were 0–1830 per 1000 m^3 (overall mean = 380 per 1000 m^3; S.E. = 80). *E. mordax* (northern anchovy) was the most abundant species at this station, followed by *H. pretiosus*-osmerid, *G. lineatus* (white croaker), *L. armatus* (Pacific staghorn sculpin), and *C. ios* (arrow goby); these taxa comprised 87% of the catch.

Seasonal peaks in larval abundance generally were characterized by the occurrence of a single taxon. At the harbour entrance station, 73% of the larvae collected in winter 1975 were *H. pretiosus*-osmerid, and 91% collected in summer and fall 1975 were *E. mordax* [Figure 2(a)]. Less distinct peaks were produced by *L. armatus* in winter 1976 and by *G. lineatus* during fall of all years. It is notable that the deep water of the Monterey Submarine Canyon influenced species composition of larvae in the slough and harbour; larvae from the mesopelagic species *Stenobrachius leucopsarus* (northern lampfish) were collected at the harbour entrance and bridge stations in January, and one larval *Bathylagus ochotensis* (deepsea blacksmelt) was caught in March at the harbour entrance station.

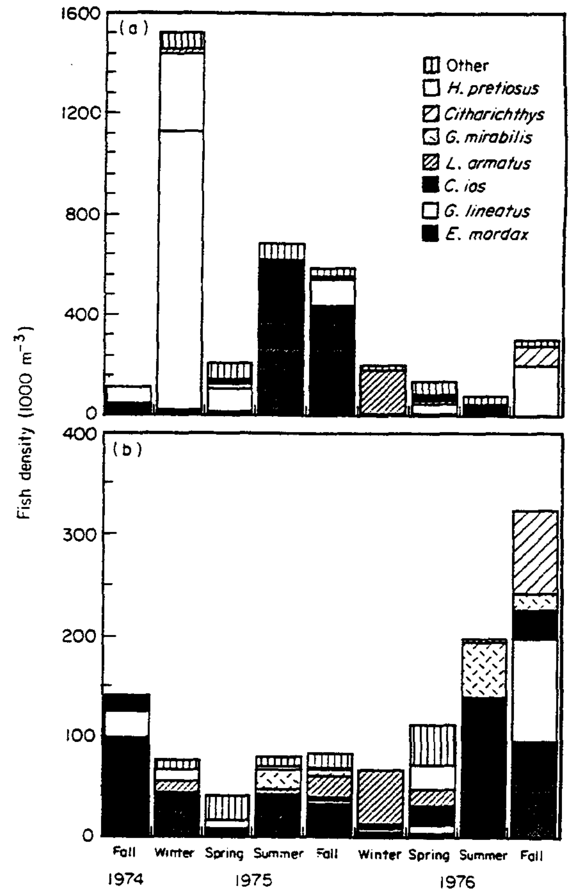

Figure 2. Seasonal average densities of dominant larval fish species collected at (a) the harbour entrance, and (b) the bridge stations in Elkhorn Slough from September 1974–September 1976.

Densities were lowest at the bridge station, ranging from 0 to 370 larvae per 1000 m^3 (mean = 130 per 1000 m^3; S.E. = 20). Sixteen species caught in 69 tows represented only 275 larvae. Eighty-nine percent of the total catch was comprised of *E. mordax*, *G. lineatus*, *C. ios*, *L. armatus*, *G. mirabilis*, *Citharichthys* spp. (sanddab) and *H. pretiosus*-osmerid, in rank order of abundance. The most prominent peak in abundance, representing *E. mordax* and *G. lineatus* larvae, occurred in late summer 1976 and early fall 1976 [Figure 2(b)]. Gobiid larvae (*G. mirabilis* and *C. ios*) also were present in large numbers during these periods. Newly hatched *Citharichthys* spp. larvae (S.L. = 2 mm) occurred in relatively high abundance (25% of catch) in early fall 1976 at both the bridge and harbour entrance stations.

Densities of larval fishes at the dairy stations also were low, ranging from 10 to 450 per 1000 m^3 (overall mean = 200; S.E. = 20). From 70 tows, 261 larvae and 15 taxa were identified. Peak abundance occurred in late summer and fall [Figure 3(a)], largely due to high numbers of *E. mordax* and *G. mirabilis*, and in winter 1976 due to *G. lineatus*, *E. mordax*, and *L. armatus*.

Overall density of larvae at the red house station was higher than at the bridge and dairy stations (mean = 290 per 1000 m^3; S.E. = 50). Average monthly densities ranged from 10 to 1 650 fish per 1000 m^3. Twelve taxa were identified from 790 larvae collected in 70 tows. Ninety-one percent of the catch comprised four species (*G. mirabilis*, *C. ios*, *E. mordax*, and *L. armatus*); nearly 70% of all larvae were gobiids. Densities were highest in fall 1974 and in summer and fall 1976 [Figure 3(b)], largely because of *G. mirabilis*. *E. mordax* larvae also contributed to the high densities in fall. *L. armatus* and *C. pallasii* (Pacific herring) were seasonally abundant in winter and spring, respectively. *C. ios* larvae occurred in every season, with greater abundance in summer and fall.

Abundance of larval fishes was highest at the Kirby Park station (monthly mean densities were from 15 to 4000 per 1000 m^3; overall mean = 770, S.E. = 130). Number of larval taxa, however, decreased with distance from the ocean, with only 12 taxa (one to six per tow) representing 1818 larvae at the Kirby Park station. Larvae of *G. mirabilis*, *E. mordax*, *C. ios*, and *C. pallasii* accounted for 93·3% of the total catch. Peaks in abundance [Figure 3(c)] primarily were due to *C. pallasii* larvae in spring, *E. mordax* in spring and fall, and large numbers of *G. mirabilis* in summer and fall (especially in September 1976 with 3520 larvae per 1000 m^3). *C. ios* were present in substantial numbers throughout the sampling period.

Species similarity

Two distinct assemblages of larval fishes were discerned using percentage similarity index and Spearman's rank correlation coefficient (Table 2). Assemblages at the red house and Kirby Park stations, the two furthest from the ocean, were most similar to each other (PSI = 0·81; $r_S = 0{\cdot}95$, $P < 0{\cdot}01$). A high degree of similarity was indicated by both indices when evaluating pairwise comparisons of species composition between the harbour entrance, bridge, and dairy stations. Species composition at stations nearest the ocean (harbour entrance and bridge) was least similar to that of assemblages furthest inland. Species comparisons between the mid-slough dairy station and either the red house or Kirby Park stations were not as conclusive. Although the rank order of species abundance was significantly similar in these comparison, PSI values were low. This indicated that the relative abundance of individual species differed between middle and upper areas of the slough, likely due to the dominance of *G. mirabilis* at the red house (57%) and Kirby Park (52%) stations (compared to 10% at the dairy station).

Size of larvae

Most larvae were relatively small and varied little in size (Table 1). *E. mordax*, *C. pallasii*, and *H. pretiosus*-osmerid had the broadest temporal or spatial size ranges. Size composition of *E. mordax* larvae varied significantly (Kruskal–Wallis; $P < 0{\cdot}01$) among stations (Figure 4). Most *E. mordax* collected at the stations closest to the ocean were less than 15 mm S.L., and the smallest larvae (< 5 mm S.L.) were abundant from June to September. *E. mordax* larvae were larger (up to 34 mm S.L.) at upper slough stations (red house and Kirby Park), and increased in length from June (3–6 mm S.L.) to March (19–32 mm S.L.). Young anchovies of the previous year class were no longer collected in plankton nets after the late spring and early summer at any station.

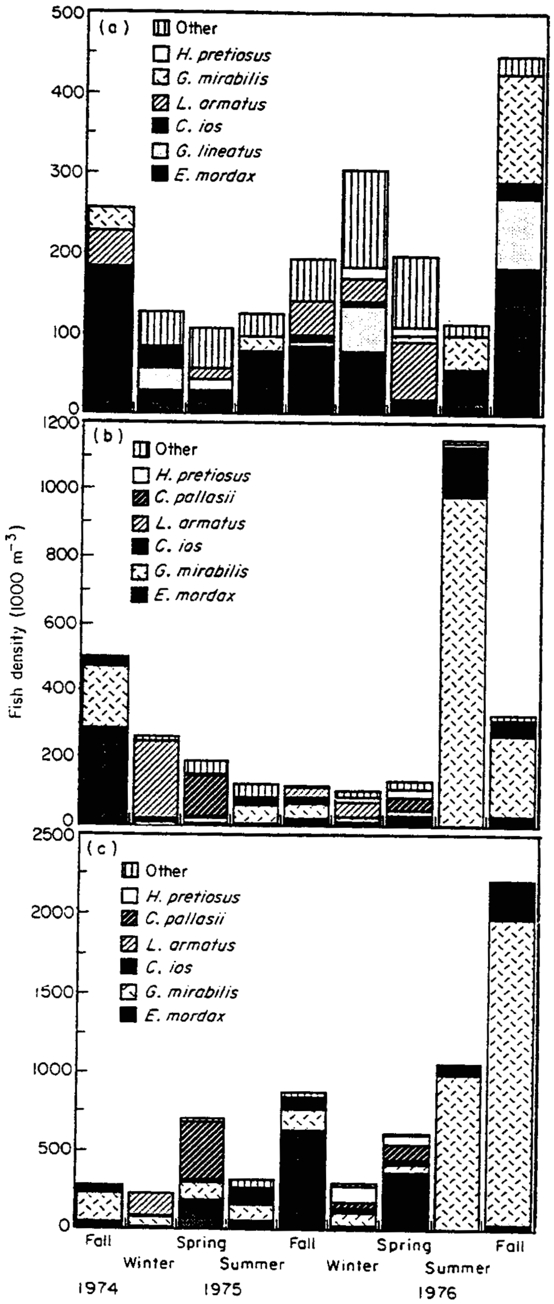

Figure 3. Seasonal average densities of dominant larval fish species collected at (a) the dairy, (b) the red house and (c) the Kirby Park stations in Elkhorn Slough from September 1974–September 1976.

TABLE 2. Bivariate Spearman's rank correlation coefficients (R_s, lower left matrix) and percentage similarity indices (**PSI**; upper right matrix) for species composition of larval fishes from five stations in Elkhorn Slough

		Harbour entrance	Bridge	Dairy	Red House	Kirby Park
				PSI		
	Harbour entrance	—	0·71	0·61	0·29	0·41
	Bridge	0·75**	—	0·80	0·44	0·49
R_s	Dairy	0·59*	0·62*	—	0·48	0·54
	Red house	0·41	0·41	0·80**	—	0·81
	Kirby Park	0·39	0·38	0·69**	0·95**	—

*Significant at $P=0{\cdot}05$; **significant at $P=0{\cdot}01$.

Size composition of *H. pretiosus*-osmerid larvae also revealed a spatial trend of larger larvae (range = 25–48 mm; median = 32 mm S.L.; $n=60$) at the Kirby Park station and smaller larvae (range = 3–6 mm; median = 4 mm S.L.; $n=117$) at lower slough stations (harbour entrance and bridge). *Clupea pallasii* larvae also had a broad range of lengths (3–28 mm S.L.; Table 1), and were abundant primarily at the Kirby Park station, where they ranged in size from 5–28 mm S.L. (median = 18 mm; $n=66$).

Eggs

The 201 samples, which were collected from October 1975 to September 1976, included 24 085 fish eggs. Ninety-four percent of the eggs were from seven taxa, including *E. mordax* (57%₀ of total abundance), *Citharichthys* spp. (19·8%), *G. lineatus* (6%), *Pleuronichthys verticalis* (hornyhead turbot), *P. coenosus* (C-O turbot), *P. decurrens* (curlfin turbot), and *Symphurus atricauda* (California tonguefish). The remaining 6%, largely 1 mm diameter eggs without oil globules (likely to be from the pleuronectid complex) and indistinguishable eggs of various sizes, were placed into the 'other' category. Only four taxa of eggs were collected also as larvae (*E. mordax*, *Citharichthys* spp., *G. lineatus*, and *P. verticalis*), of which two (*E. mordax* and *G. lineatus*) were among the eight most abundant larvae.

Density was highest in summer, largely because of numerous eggs of *E. mordax* at the three most seaward locations (Table 3). *E. mordax* eggs essentially were absent from the slough in winter and spring (November–April). In general, fish eggs were most abundant at the bridge station, decreasing dramatically in number toward the upper slough (the red house and Kirby Park stations). Eggs of *Citharichthys* spp. were collected year-round throughout the slough, with high abundance in summer and fall at lower slough stations (harbour entrance and bridge). Density of *Citharichthys* spp. eggs peaked later (October) at upper slough locations, exceeding that of *E. mordax*. Eggs of *G. lineatus* also were collected throughout the slough, but in relatively high numbers only at the two stations closest to the ocean; peak abundance occurred in fall and early winter, with few eggs found

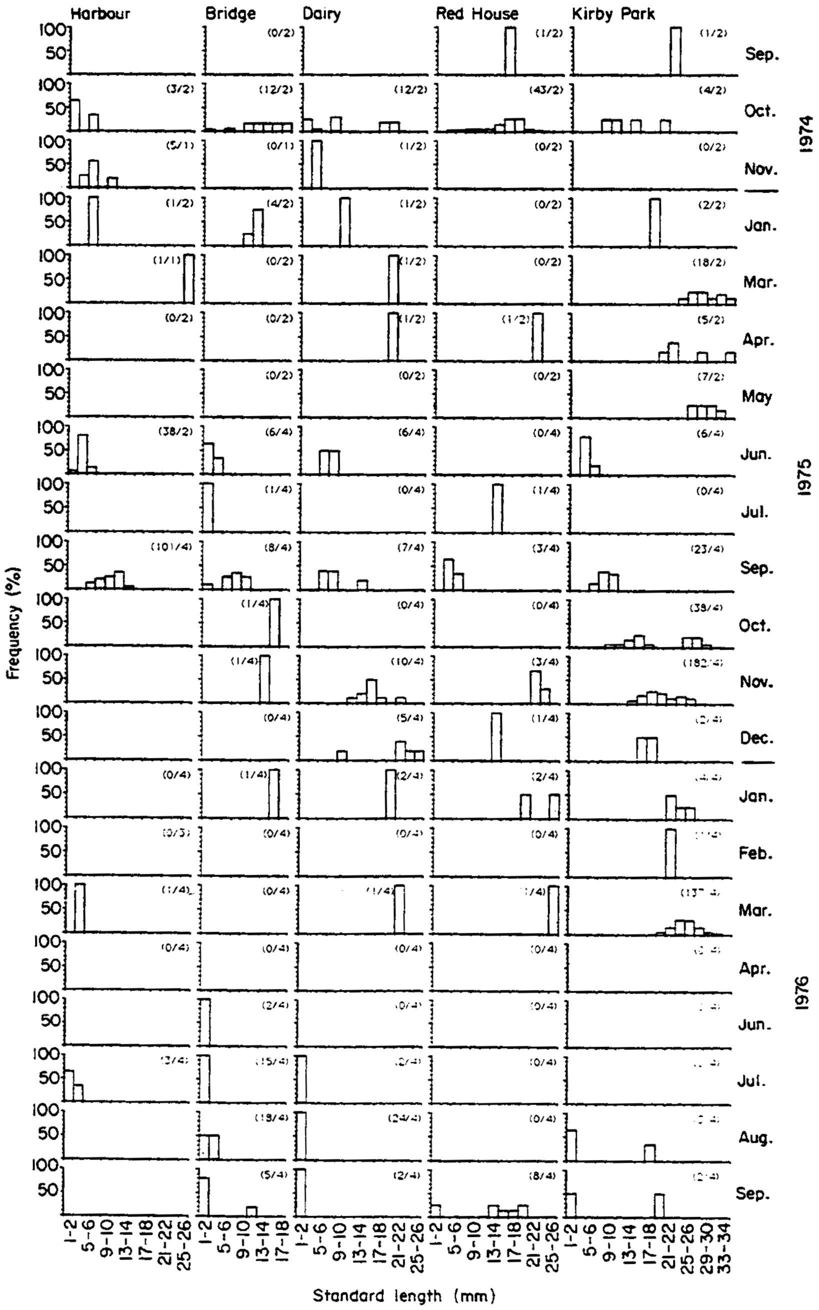

Figure 4. Length–class frequency distributions of *Engraulis mordax* larvae collected at five locations within Elkhorn Slough, CA; number of larvae/number of samples are shown.

TABLE 3. Seasonal average density (number per m^3) of fish eggs collected at five locations in Elkhorn Slough, CA

Station/taxa	Fall	Winter	Spring	Summer
Harbour entrance				
Engraulis mordax	0·6	—	0·1	9·4
Genyonemus lineatus	0·7	—	0·4	—
Citharichthys spp.	1·7	T	0·1	2·7
Pleuronichthys verticalis	—	—	T	T
P. coenosus	—	T	T	T
P. decurrens	—	—	T	—
Symphurus atricauda	0·1	—	—	T
Others	2·0	T	0·1	2·7
Total	5·1	0·1	0·7	14·9
Bridge				
Engraulis mordax	5·1	T	0·1	26·8
Genyonemus lineatus	0·9	0·8	0·6	—
Citharichthys spp.	2·0	0·3	0·1	4·8
Pleuronichthys verticalis	0·1	T	T	0·1
P. coenosus	—	—	T	T
P. decurrens	T	—	—	—
Symphurus atricauda	T	—	—	—
Others	1·7	T	0·1	1·9
Total	9·8	1·1	0·9	33·6
Dairy				
Engraulis mordax	4·5	T	T	12·1
Genyonemus lineatus	0·4	0·5	0·1	T
Citharichthys spp.	3·3	1·3	0·3	2·6
Pleuronichthys verticalis	T	T	—	T
Others	1·7	T	T	1·1
Total	9·9	1·9	0·4	15·8
Red House				
Engraulis mordax	0·3	—	—	0·4
Genyonemus lineatus	T	0·1	T	—
Citharichthys spp.	1·5	0·3	0·3	0·1
Others	T	T	T	0·1
Total	1·9	0·4	0·3	0·6
Kirby Park				
Engraulis mordax	0·1	—	—	0·1
Genyonemus lineatus	T	T	—	—
Citharichthys spp.	0·3	0·2	0·1	0·2
Others	—	T	—	—
Total	0·4	0·2	0·1	0·3

A trace density (T) is less than 0·1 per m^3; — means no eggs of that species were collected.

after March. *Pleuronichthys* spp. eggs had no seasonality, occurring in small numbers only at lower slough stations. Very low numbers of *S. atricauda* eggs were collected in summer and fall only at seaward stations.

Reproductive specialization

Six larval fish species were classified as resident (Table 1), of which five have demersal eggs and one [*Syngnathus leptorhynchus* (bay pipefish)] is live-bearing. Greater than 69%

of the total number of larvae were from demersal eggs; 56% of the larval abundance was classified as slough resident. Six species, and nearly 35% of the total abundance, were from marine immigrant adults. Fifteen species, representing <7% of the total abundance, were considered to be of marine origin.

Discussion

There are similarities in species composition among Elkhorn Slough larval fish assemblages and those described in the few comparable studies of other west coast estuaries. Gobiid and clupeoid larvae dominated the catch in most systems. *Lepidogobius lepidus* (bay goby) and *C. pallasii* were analogous to *G. mirabilis* and *E. mordax* (the two dominant species in Elkhorn Slough), and accounted for 82% and 90% of all larvae collected in Humboldt Bay (California's northernmost estuary; Eldridge & Bryan, 1972) and Yaquina Bay, Oregon (Pearcy & Myers, 1974), respectively. *L. armatus*, *C. ios*, and osmerid larvae similarly contributed to the assemblages in Humboldt Bay (13% of the catch) and Elkhorn Slough (21·4%). *L. armatus* and *H. pretiosus* also were relatively abundant in Yaquina Bay. Ichthyoplankton assemblages of almost all southern California bays and estuaries are dominated by engraulid eggs (*Anchoa* spp.) and gobiid larvae (McGowen, 1977; Leithiser, 1981; Nordby, 1982; Horn & Allen, 1985). Numerical importance of engraulid larvae [(*Anchoa* spp. (18·5%) and *E. mordax* (9·6%)] was second only to gobiids (38·8%) in upper Newport Bay (Horn & Allen, 1985). Sciaenid larvae were abundant only in Elkhorn Slough (*G. lineatus*) and bays to the south.

The limitations of ichthyoplankton surveys should be considered when describing habitat use by fishes. The number of egg and larval taxa collected in Elkhorn Slough is limited by species identification (e.g. taxonomic problems with larval gobiids, atherinids, and *Sebastes* spp.). Of the 32 taxa of fish eggs and larvae collected in Elkhorn Slough, eight were considered common (each representing >1% of the total catch). Sixty-five species of juvenile and adult fishes have been collected in the slough, of which 40 have abundances >1% of the catch at any one station (Yoklavich *et al.*, 1991). Underestimates of the number of taxa and densities of individuals also result from avoidance of gear by larger larvae during daytime sampling and extrusion of small newly-hatched larvae. We expected to minimize avoidance by operating a pushnet without preceding bridles in relatively shallow (2–5 m) turbid (0·5–4·5 m visibility) water. Sampling at night could increase total numbers of some species, especially the already-abundant gobiids (Leithiser, 1981; Whitfield, 1989). Although the main channel of Elkhorn Slough is shallow and well-mixed, especially seaward of the tidal prism (Broenkow, 1977), the pushnet was limited to the upper 1-m of the water column and therefore inadequate for sampling epibenthic and shallow tidal creek habitats. Samples of juvenile fishes from tidal creeks of Elkhorn Slough (Yoklavich *et al.*, 1991) comprised species that also were abundant in the ichthyoplankton survey (*E. mordax*, *L. armatus*, and the gobiids), but the second most abundant species (*A. affinis*) only ranked tenth in ichthyoplankton samples.

Reproductive specialization (i.e. egg type and spawning origin of adults) also influences descriptions of fish assemblages from egg and larval surveys. Adhesive, demersal eggs are common to resident fishes of Elkhorn Slough and are not collected in plankton samples. Pearcy & Richards (1962) noted a predominance of larval fish species from demersal eggs in the Mystic River estuary, and suggested that this aided in retention of eggs within the system. This specialization assists in maintaining adult populations in areas of discontinuous habitat. Embiotocids (seven species of surfperch) are the most abundant group of adult fishes in Elkhorn Slough (Yoklavich *et al.*, 1991). Because embiotocids are viviparous and extrude well-developed young, eggs and larvae are not available to ichthyoplankton surveys. Similarly, three species of viviparous marine *Sebastes*, which release larvae offshore, were collected only as juveniles in otter trawls at near ocean stations (Yoklavich *et al.*, 1991). The young of several species of viviparous elasmobranchs, classified as partial-residents, also are not sampled with ichthyoplankton gear.

Two seasonal groups of larvae are distinguished from ichthyoplankton samples in Elkhorn Slough. *E. mordax* and gobiids (*G. mirabilis* and *C. ios*) form a late-summer and early-fall group. *E. mordax* were abundant also in winter, but these were mainly post-flexion larvae and early juveniles that were overwintering at the Kirby Park station. Both dominant gobiids have protracted spawning seasons (from February to September) that peak in late summer (Weisel, 1947; Prasad, 1948). Abundance of gobiid larvae increased with rising water temperatures throughout the slough, reaching maximum densities at 18–20 °C for *C. ios* and 19–23 °C for *G. mirabilis.*

Although some spawning of *E. mordax* occurs in coastal waters throughout the year (Ahlstrom, 1966), the central California subpopulation (offshore from San Francisco Bay to Point Conception) has a broad spawning peak from February to April (Parrish *et al.*, 1985), when mean water temperature is 14–16 °C (Smith & Lasker, 1978). Peak spawning of the northern subpopulation off Oregon and northern California is later (mid-June to mid-August), and at similar water temperatures (Richardson, 1980). Size distributions of larval *E. mordax* and spatial and temporal patterns of egg densities in Elkhorn Slough indicate that spawning occurs primarily at lower slough stations or in adjacent bay water in summer and early fall (July through August). A narrow band of warm (> 14 °C) water persists along the eastern edge of Monterey Bay, adjacent to Elkhorn Slough, beginning about July (Breaker & Broenkow, 1989), and coincides with our largest catches of *E. mordax* eggs in lower slough areas. Most *E. mordax* larvae were collected in slough water from 14 to 18 °C. This is similar to peak spawning in San Francisco Bay (from July–September) when mean water temperatures are 19–19·8 °C (McGowan, 1986).

While more speciose, a winter and early-spring group that included *L. armatus*, *H. pretiosus*-osmerid, two species of the silverside family Atherinidae, and *A. hexapterus* (Pacific sandlance) was not as abundant as the summer–fall assemblage. The winter–spring group was more variable in occurrence; pulses of high numbers of preflexion osmerid and *A. hexapterus* larvae were collected in single tows. Although *C. pallasii* larvae were seasonally abundant in the upper areas of Elkhorn Slough in the spring, the lack of adequate spawning substrate, such as extensive *Zostera marina* (sea-grass) beds, potentially limits use of the lower slough as nursery habitat. Submerged aquatic vegetation is relatively sparse in Elkhorn Slough, except for dense *Salicornia virginica* (pickleweed) in the intertidal marsh zone (1·8 m above MLLW) of the upper slough. Recent restoration of seagrass beds in Elkhorn Slough could modify distribution and enhance recruitment for those species with demersal, adhesive eggs.

The temporal occurrence of *G. lineatus* larvae in Elkhorn Slough corresponded to their spawning season from late-fall to spring off southern California (Goldberg, 1976; Watson, 1982), and to the presence of eggs from fall through spring at stations closest to the ocean. All *G. lineatus* larvae were very small (2–4 mm) and abundant only at locations west of the tidal prism, suggesting transport from the slough during early development. Most *G. lineatus* larvae in southern California were collected in coastal water within 4 km from shore (Watson, 1982).

Seasonal patterns of larval fish abundance were similar in many of the west coast studies of inshore larval fish assemblages. Peak abundance of all larvae in Yaquina Bay, Oregon occurred in winter and spring, largely due to high numbers of *C. pallasii*; highest densities of the co-dominant *Lepidogobius lepidus* occurred in summer. In Humboldt Bay, California high larval abundances in January–February and in April–May were produced by species that formed the winter–early spring group in Elkhorn Slough (Eldridge & Bryan, 1972). Because Humboldt Bay did not have large populations of larval *E. mordax* or *G. mirabilis*, a summer–fall increase in abundance was not obvious; however, the number of *C. ios* increased in October. Highest numbers of larval fishes occurred in May and September in southern California's upper Newport Bay, largely due to *Anchoa* spp., *E. mordax*, *C. ios*, and other gobiids (Horn & Allen, 1985).

Preflexion larvae of pleuronectiform fishes essentially were absent from Elkhorn Slough, Humboldt Bay (Eldridge & Bryan, 1972), and Yaquina Bay (Pearcy & Myers, 1974). However, one large pulse of newly-hatched *Citharichthys* spp. larvae was sampled in September 1976 at the three stations closest to the ocean in Elkhorn Slough, and *Citharichthys* spp. eggs were found at all times of year throughout the slough in relatively high numbers. Newly-settled juvenile flatfish [e.g., *Parophrys vetulus* (English sole), *Citharichthys stigmaeus* (speckled sanddab), and *Platichthys stellatus* (starry flounder)] can be abundant in the three embayments (Horn & Allen, 1976; Boehlert & Mundy, 1987; Yoklavich *et al.*, 1991). *Parophrys vetulus* spawn offshore, and metamorphosing larvae (about 15–23 mm S.L.) recruit to bays and estuaries (Boehlert & Mundy, 1987). Boehlert & Mundy (1988) suggested that physical and behavioural factors that are related to tidal flux operate in the recruitment and retention of larval and juvenile fishes in estuaries. *Citharichthys* spp. and *P. stellatus* juveniles may recruit in a similar manner, although gravid *P. stellatus* have been collected in inshore areas that have little tidal flushing and in upper areas of tidal creeks in Elkhorn Slough.

The decrease in number of larval taxa with distance from the ocean occurs as well in other bays and estuaries. Fewer taxa were collected at Humboldt Bay's most inland stations, which had higher variability in temperature and freshwater input (Eldridge & Bryan, 1972). Number of taxa was maximum at the mouth of Yaquina Bay and decreased up the estuary (Pearcy & Myers, 1974). In Elkhorn Slough, greater seasonal fluctuations in water temperature and salinity occur at upper slough stations (red house and Kirby Park; Figure 5), potentially limiting the number of taxa able to utilize this area either as spawning or nursery grounds. Marine species, such as *G. lineatus*, *A. hexapterus*, *Sebastes* spp., and most flatfishes, spawn offshore. When these larvae, and in some cases eggs, occur in the slough, it is primarily in the lower slough, undoubtedly transported onshore by surface currents.

The occurrence of larvae of the deep-dwelling fishes *Stenobrachius leucopsarus* and *Bathylagus ochotensis*, categorized as offshore species (Boehlert *et al.*, 1985), was not unexpected in samples from the harbour entrance station during winter and early spring, because net flow of water over Monterey Submarine Canyon is believed to be up-canyon (onshore) most often (Breaker & Broenkow, 1989). Larvae of mesopelagic species also were collected at the mouth of Humboldt Bay (Eldridge & Bryan, 1972) and in Yaquina Bay during the winter period of onshore transport (B. C. Mundy & G. W. Boehlert, unpubl. data).

Although inland slough regions had fewer taxa, they contributed the greatest numbers of individual larvae. Resident gobiids were the most abundant larvae in the slough; their rank abundance increased with distance from the harbour entrance. Adults and juveniles

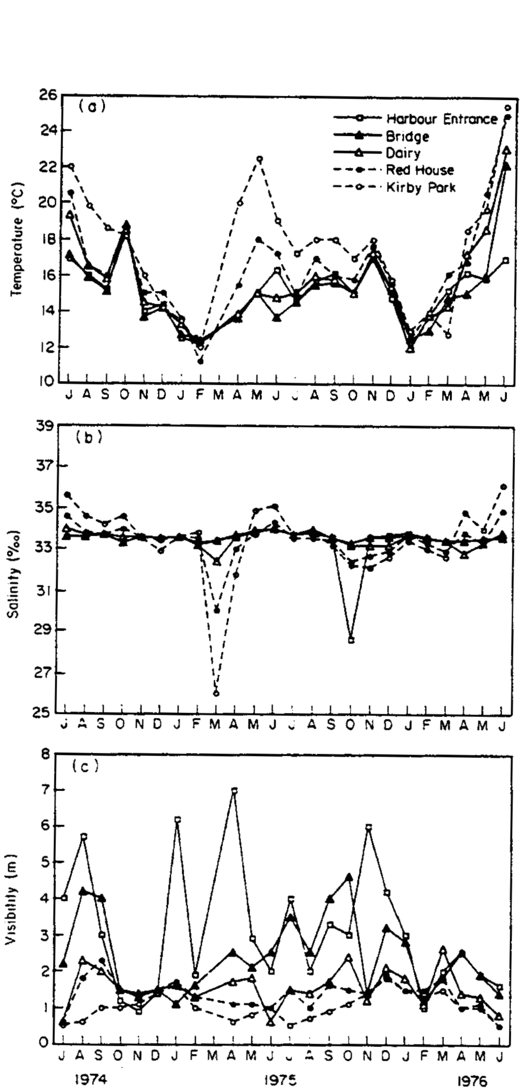

Figure 5. Average monthly water (a) temperature, (b) salinity, and (c) visibility at five locations in Elkhorn Slough, CA from July 1974 to June 1976 [data from Broenkow (1977)].

of *G. mirabilis* and *C. ios* were collected almost entirely in tidal creeks and inland slough regions (Barry, 1983; Yoklavich *et al.*, 1991). Mudbanks and extensive *Salicornia* spp. beds bordering these regions provide suitable habitat for spawning gobiids.

Along with localized spawning habits of adults, hydrographic conditions in Elkhorn Slough contribute to the dominant spatial patterns in abundance of fish eggs and larvae. Significant differences between lower (harbour entrance and bridge) and upper (red house and Kirby Park) slough assemblages suggest that the tidal prism (about 4·8 km from the harbour entrance) assists in retaining some species within the slough. Elkhorn Slough receives little freshwater runoff, except during winter months of non-drought years. Mid-slough (dairy; 3·1 km from harbour entrance) species composition was in transition between lower and upper groups. Water is exchanged daily by tidal currents, and seasonal variations in temperature and visibility are similar at harbour entrance, bridge, and dairy stations (Figure 5; Broenkow, 1977). The most abundant larvae at these stations were very small preflexion *E. mordax* and *H. pretiosus*-osmerid, both classified as marine immigrants. Newly hatched *G. lineatus*, a marine species with pelagic eggs, also was abundant at the most seaward stations, suggesting advection of eggs and larvae into the slough rather than spawning *in situ*. The water mass to the east of the tidal prism (red house and Kirby Park stations) fluctuates widely in temperature and salinity, and has lower visibility (Figure 5). Newly hatched *E. mordax* are distributed progressively eastward to the Kirby Park station, and seemingly thrive in the shallow upper slough, as indicated by increased length distributions from September to March. Zooplankton samples collected in a 135 µm mesh net concurrently with the larval fishes at the upper slough stations in late spring, summer, and early fall contained high densities of potential prey, such as barnacle nauplii, polycheate larvae, and all stages of the copepods *Acartia* spp. and *Oithona spinifera* (Cailliet *et al.*, 1977; Pace, 1977). The high water residence time (greater than 300 days; Smith, 1973), and increased summer water temperatures (Figure 5), potential zooplankton prey densities, and available substrate for adhesive demersal eggs in shallow inland marsh habitats of the slough enhance reproductive success, larval retention, and survival.

From earlier studies of juveniles and adult fishes (Barry & Cailliet, 1981; Yoklavich *et al.*, 1991) and the present ichthyoplankton survey, the relatively small area of Elkhorn Slough serves as spawning and nursery grounds for several species of transient marine fishes and at least six species of resident estuarine fishes. Five of the ten most abundant species of larval fishes are of commercial importance, either directly (e.g. *E. mordax*, *C. pallasii* and *Citharichthys* spp.) or indirectly as forage for other commercial species (e.g. osmerids and atherinids). While Elkhorn Slough's contribution to nearshore fish assemblages is limited by size, the spatial and temporal patterns in larval fish abundance are important for further assessment of the linkage between inshore productivity and Monterey Bay.

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